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SPECIATION IN LIMPETS OF THE GENUS *ACMAEA*

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INTRODUCTION

THE occurrence within a circumscribed area of several closely related but distinct species of organisms poses many difficult questions about their possible mode of origin. A particularly puzzling example of this kind is presented by the limpets of the genus *Acmaea.* Along the Pacific coast of North America, indeed within the limits of the state of California, there dwell no less than seventeen species of the genus *Acmaea* (A. R. Test, MS). Further, they all live within the very narrow vertical limits of the intertidal zone along the ocean shore. The problem of the mode of origin of this diverse group of species deserves intensive study.

Of the seventeen species living along the coast of California, eight range both north and south beyond the limits of the state, although not all their ranges extend the entire length of the west coast of North America. These species are *pelta* Eschscholtz, *digitalis* Eschscholtz, *asmi* (Middendorff), *paleacea* (Gould), *rosacea* Carpenter, *limatula* Carpenter, *scabra* (Gould), and *triangularis* Carpenter. Two others, *insessa* (Hinds) and *mitra* Eschscholtz, have been accorded very lengthy ranges, but I have not been able to substantiate these ranges from the collections I have seen. The ranges of the seven remaining species terminate within the state of California, but extend beyond one border, either to the north or the south. The species ranging north of the state of California are *testudinalis scutum* Eschscholtz, *persona* Eschscholtz, *depicta* (Hinds), *instabilis* (Gould), *fenestrata cribraria* (Gould), and *ochracea* Dall; *conus* Test (1945 *a* and *b*) ranges south of California.

There is actually a brief area along the coast of California, extending from Point Concepcion south to Point Fermin (San Pedro), where all seventeen of these species are present. When the narrow limits of the intertidal zone are taken into consideration, this is remarkable and very difficult to explain on the basis of complete geographic isolation for every species at some previous time in order to permit speciation to develop.

These species came into existence in this limited area in part because of the extremely limited movements of each animal during its lifetime, in part because of the relative rigidity of the microhabitat limitations of each species. These two factors have permitted speciation to take place by geographic isolation of the usual type and also by ecologic segregation of an unusual type, in which isolation may be a matter of only inches, or at most a foot.

Although I worked with the group originally only from the taxonomic point of view, I became interested in the problem of the origin of several species in a limited area. As my studies of the natural history of the group proceeded (A. R. Test, 1945*c*), ideas suggested how such a situation came to exist, and it seems worthwhile to present them here, as pertaining not only to the group under consideration, but perhaps also to other groups.

The study of which this paper records the results was carried out under the guidance and with the encouragement of Professor S. F. Light at the University of California, to whom I wish to express my very great gratitude.

The specific nomenclature used in this paper follows that in a manuscript which will be published under the title, "The Taxonomy, Natural History, Phylogeny, and Bibliography of the Genus *Acmaea.*"

TERMINOLOGY

In order that there will be no misunderstanding as to what is meant in this paper by certain terms which have been used differently by previous authors, I define my usage for each term.

SPECIES is here understood to mean a morphologically distinguishable and interbreeding group of animals which do not appear to interbreed with any other morphologically distinguishable group, since no intergrades have been found.

A SUBSPECIES, the only category for which a trinomial name will be used in this paper, is always a geographic race, as defined below. No other group of variants and no individual variants will be given a trinomial name. For the sake of clarity, variants which have received names in the previous literature are discussed and synonymized in the manuscript already cited.

SPECIATION is here understood to mean those processes during which divergence is established and reproductive isolation is accomplished so that a "parent species" breaks up into two or more daughter species (May, 1942: 23).

GEOGRAPHIC SPECIATION is that differentiation which has developed during a recognizable and measurable geographic isolation of the parent and offshoot stocks from each other, by the gradual accumulation of inherited differences which make morphological distinction and which prevent interbreeding.

ECOLOGIC SPECIATION is that differentiation which has taken place during isolation of extreme variants which could not survive in the parental microhabitat, but which are able to take over a microhabitat not compatible with the parental morphology and ecology. This isolation is not of a geographic type, but is due to the unsuitability for the parent stock of the microhabitat invaded by the offshoot, and to an intervening area, however small, which cannot be crossed by individuals of either stock, such as is provided by the holdfasts of some of the algae and by silt and sand surrounding the base of the rocks or plants occupied by the offshoot stock.

An ECOLOGIC VARIANT is a nonhereditary phenotype which differs from most members of the species in some definite, recognizable manner. For example, in bays or harbors, where the wave action is slight but the chemical contents of the water are heavily concentrated with industrial wastes or detritus from organic sources, individuals of all species represented have heavier than normal shells, humped-up shape, with reduced aperture, and increased ornamentation. Such variations predominate in all species wherever such areas occur.

INDIVIDUAL VARIANT refers to a phenotype produced by a particular combination of hereditary traits.

EURYTOPIC refers to a broad tolerance of diverse environmental conditions on the part of a species population. Such species are able to survive in many recognizably diverse situations, the microhabitat having only broadly recognizable limits.

STENOTOPIC refers to a rigidly restricted tolerance to variation in environmental conditions on the part of a species population. Such species are found only in one particular kind of microhabitat, always the same in all or most all of its recognizable features.

LIMITING CONDITIONS are those factors in the habitat to which the individuals must adapt or fail to survive.

DOMINANT SPECIES, FORMS, OR VARIANTS are those which are most abundant in the area or region under discussion.

FIELD STUDIES

Field studies were conducted along the coast of California, for a period of six years (1931 to 1937). Visits were made to every important, and many small, reefs, as well as to estuaries, sloughs, and river mouths, from the northern boundary of the state south to Point Fermin, San Pedro, California. Certain situations were visited repeatedly, the most frequently worked over being Moss Beach, San Mateo County; Monterey; Jenner, Sonoma County; and the reefs between and around Bolinas and Tomales Bay, Marin County. Special trips were made to work at and near Points Concepcion and Arguello, Santa Barbara County.

CRITERIA FOR SPECIES

For working out the relationships of the various species of limpets, I have not found the shell a reliable guide, probably because it bears the brunt of environmental contact. It is particularly susceptible to the development of adaptive characters and hence liable to both convergent and divergent evolution. The shell of a limpet is always in contact with the environment, is the part of the animal most likely to be affected by it, and, therefore, is least likely to indicate relationships accurately. Direct contact with the environment has resulted in numerous ecologic variants, many of which, under special conditions, have become dominant in given localities. These variants have added to the confusion in the relationships of the taxonomic forms.

The unreliability of the shell for showing taxonomic relationships is well illustrated by the fact that limpets in similar ecologic situations the world over have shells of practically the same general contour, size, weight, and often sculptural pattern. This parallelism is so general that on the basis of the shell alone it is frequently possible to determine the ecologic situation from which any given species or group of individuals may have come. It is hardly necessary to add that species geographically far removed from each other, although equivalently situated ecologically and possessing similar shell characters, are not likely to be closely related. Instead, a given species will be more closely related to another often very different in architectural pattern of shell but occupying the same or adjacent geographic areas than to species with architecturally equivalent shells but living in widely separated geographic ranges.

A slightly less significant illustration is provided in shell characters by predictable variations on the basis of ecologic influence. Some individuals of a species living under ecologic conditions different from the normal in some controlling factor or factors will often differ in certain characters from normal individuals in a particular manner. Such variations are predictable in connection with known variable ecologic factors which result in conditions below optimum for the species. Among the well-established species on the coast of California it is not uncommon to find the same architectural principles being utilized within several normally very different species by individuals subjected to the same kind of unfavorable environmental conditions, such as lowered salinity, increased chemical content of the water, or increased wave action.

Obviously, this tendency to vary with the ecological situation practically eliminates the shell as a factor in determining species relationships and necessitates the use of some other structure that is more dependable than the shell for defining these relationships. The structure must not be too plastic under ecologic influences, nor yet so completely removed from the environment as to prevent accumulation of small specific changes. The basal ribbon of the radula appears to be such a structure.

The radula, well enough protected from outside influences during its development, later regularly is in contact with a specific part of the environment, namely, the food and its substrate. This, significantly, is the least variable part of a limpet's environment, owing to the specific nature of the feeding habits of most limpets. Hence, there is little tendency for the radula to vary within species. In the past, use of the radula has been limited to a study of the teeth, which provide poor criteria for specific determination because of change due to injury and wear. I have used the basal ribbon of the radula, stripped of teeth; it offers a reliable basis for identification as well as for the determination of specific relationships, because it is not especially subject to selective action, injury, or wear and tear. The ribbons appear to have acquired specific characters chiefly because of the inevitable accumulation of small inherited differences.

As suggested above, the use made of the radula in the past has been open to criticism, due largely to the methods employed. Dall (1871) wisely based his subgenera of *Acmaea* upon radular characters, but unwisely used tooth shape and arrangement as the criteria for specific differentiation. Oliver (1926) made groupings of species, which he called genera, differentiated partly by tooth characters. The validity of his results was further weakened by the use of a combination of structural characters of the shell with radular characters for generic criteria. Since shell characters are not reliable indices of relationships, genera based upon them, even though in combination with radular characters, are of dubious value.

Because of these difficulties with a structure which should present ideal material for specific differentiation, J. A. Perino, of the University of California, several years ago worked out a method of preparing the radula to eliminate the weaknesses mentioned above, and to make use of the taxonomic possibilities of the structure. In a properly treated radula the teeth can easily be scraped off, the basal ribbon stained, and a thoroughly useful, specifically stable structure obtained which shows excellent specific differentiation. It is this structure, the basal ribbon, which I have used. A complete description of the preparation of the radular ribbons will appear in a subsequent paper (A. R. Test, MS).

An ambitious attempt was made to obtain length-to-width-to-height proportion ratios of the shells for the various species in order to use them in determining the specific limits, but the only result of the tedious measuring of approximately three thousand individuals of several species was the conclusion that size and proportion in limpets are too much influenced by ecologic irregularities to have any practical significance.

Each species which I recognize (A. R. Test, MS) has been diagnosed on the basis of criteria indicated as reliable by comparison of shell characters with radulae. Many of the species exhibit variability (genetic and /or somatic), either ecologic, individual, or geographic in character. In the past, this extensive variability has led to the subdivision of these species into many categories (so-called subspecies, varieties, forms). Most of these have no place in a nomenclatural system, since they are based upon differences which are not geographically segregated and seem to have no correlation with ecologic or physiologic segregation or tendencies thereto. Indeed, these categories often have been used for mere variants representing naturally occurring diversities in genetic combinations in a large heterozygous population, as well as for variants resulting from the adaptability of the individual to differing environmental conditions and to variations produced by extraneous causes (fungus infection, unfavorable environmental conditions, substrate limitations, and injuries).

Related species should manifest their relationship by any feature in inverse ratio to the amount of divergent adaptive evolution which that feature has undergone. Such is, indeed, the situation among the species of *Acmaea.* The extent of resemblance of the shells of related species depends not upon closeness of relationship, but rather upon whether or not the diverging species have remained in similar microhabitats. The radular ribbon on the other hand, less subject to adaptive evolution than is the shell, and hence not subject to the phenomena of rapid divergent or convergent evolution, indicates the actual relationship fairly accurately, regardless of whether the species in question have remained in equivalent microhabitats or have become adapted to differing situations.

METHODS OF SPECIATION

The importance of geographic subspeciation has long been understood, namely, that it seems frequently to lead to the origin of species. This appears to be the case when geographic subspecies are isolated from the main stock long enough for evolution to proceed to the point at which the isolated group can or will no longer interbreed with the main stock. Students of the genus *Acmaea* do not appear to have grasped this fact and have classed as subspecies any striking variant, regardless of its geographic coincidence with the main stock of the species, that is, with the other so-called subspecies. Every subspecies (geographic race) obviously must occupy a range which is geographically complementary to that of other subspecies of the same polytypic species (*rassenkreis* of Rensch, 1934), except within a limited area of intergradation.

To be sure, any individual phenotype common in one subspecies may appear as an occasional phenotype in any other subspecies of the same species, but each subspecies will be composed for the most part of phenotypes which appear only infrequently in any other subspecies. The bulk of the population of one subspecies differs from the bulk of the population of any other subspecies of the same species with regard to those phenotypes which predominate. Thus, a sample of any subspecific population may be recognizable by its proportions of phenotypes rather than by peculiar kinds of phenotypes. Effective isolation is then necessary over a sufficiently extended period to permit completion of the process of speciation.

Within the genus *Acmaea*, much speciation has apparently been due to the geographic process. This is indicated by the geographic ranges of some of those species which have been shown by studies of the radular ribbons to be closely related, as well as by those *Acmaea* polytypic species which are extant today.

Geographic speciation, has apparently not been the only kind to occur within the genus; indeed, it has probably been the less common type. A careful survey, including ecologic and relationship studies, of species of *Acmaea* occurring on the coast of California, has in certain instances failed to yield the slightest evidence in favor of geographic speciation. The information obtained has even suggested that such a method could not have been possible. For example, along the west coast of North America occur nine species of one subgenus (*Collisella*) affording every indication of close relationship, yet having either completely concurrent or encompassed ranges. Inasmuch as the obviously parental form has the greater range in every instance in which the range of one species is encompassed by that of another, and since the range and population midpoints of the species (Schenck and Keen, 1936) do not differ, it becomes practically impossible to explain the situation in terms of geographic speciation.

This study, however, has shown that in every example in which the related species have concurrent (or encompassed and encompassing) ranges the microhabitats are not equivalent. In fact, the microhabitats are so different that the various species are unable to invade each other's microhabitat and furthermore are isolated from one another by barriers as effective as a geographic separation, though very small in size. This isolation is emphasized by the relatively slight motility in animals of this genus.

Studies have indicated that the limpet moves during its lifetime at most within a circumscribed area of a few feet. Its limited movements are apparently for the purpose of finding food and are at rather infrequent intervals. Individuals of two species customarily return to their starting point at the end of one of their forays (Hewatt, 1940; A. R. Test, 1945*c*), whereas individuals of other species fail to do so (Richardson, 1934; Villee and Groody, 1940; F. H. Test, 1945). Whether or not a return to a home site is made, the distance traversed by any limpet within its lifetime is very limited, actually, to an area of a square foot or two at most. Consequently, there is great isolation of adults, and mating opportunities are largely limited to near-by individuals. There is further limitation of movement by substrate, since few individual limpets will leave a suitable subtrate to venture upon an unsuitable one, even in the search for a new feeding ground.

The presumably ancestral species in every instance is a species of greater variability and greater ecologic tolerance than the presumably descendant species, and the ancestral species includes among its variants some which approach the general structural lines of the descendant species. These facts provide the basis for an apparently satisfactory solution of the speciation problem in this group. They suggest that speciation in such cases has been caused by ecologic segregation of particular extreme variants of a variable species within a microhabitat different in its controlling factors from that of the parental species, and their effective isolation thereby. These variants are such as could not survive within the normal confines of the parental microhabitat, but are able to invade some other microhabitat unoccupied by and unavailable to less extreme members of the parental species. Released from the pressure of population and isolated from other variants of the parental species by sharply delimiting ecologic barriers and by the lack of motility, these variants should provide material for selective and geologically rapid development of a new form which could attain the qualifications of a new species.

Such a process as speciation by ecologic segregation depends, however, upon certain assumptions. Most important are those with regard to breeding habits. If speciation has proceeded by the gradual process of selection of mutations and extreme variations, complete segregation of the new variant from the parent stock must have been effective to permit final fixation of the characters of the new species. This would be the case if the mutations involved prevented cross breeding of the mutants and the parent stock, or if the type of fertilization required close approximation of male and female, although not necessarily internal fertilization.

Curiously enough, the literature is very contradictory with regard to the method of insemination in *Acmaea*. It is Willcox' opinion (1898: 444; 1905: 332–33) that, possibly, the limpet possesses an intromittent organ in the renal papilla, and that, probably, mantle cavity fertilization takes place. Her evidence is neither conclusive nor convincing, but her belief is mentioned for what it is worth. Boutan (1898: 1887–88) definitely stated that fertilization is not by copulation, but occurs free in the water. This statement is based upon his work on the development of *A. virginea,* but he failed to give his grounds, and the statement is in complete disagreement with that of Willcox. He stated that the eggs are laid singly and immediately washed out into the water, whereas Willcox stated that they are laid in a mucous strand. These contradictory statements may be based on observations made upon different species. The situation is complicated by the possibility that Willcox, as she suggests, may have seen unfertilized eggs laid, and Boutan may have seen eggs which had already been fertilized in the mantle cavity but which did not start development until laid. Thiem (1917: 597) made the statement that he believed internal fertilization to be very unlikely because of the large number of sperm produced, but this is not pertinent evidence. Fischer in 1863 is said (Willcox, 1905: 332) to have made the statement that he had found the ovaries of *Patella* filled with embryos already provided with a shell, which would be strong indication of true internal fertilization. However, he (1863: 321) actually said: " . . . on trouverait l'ovaire des femelles rempli d'oeufs ou peut-être même d'embryons déjà pourvus de coquille." Dall (1879), likewise, believed that internal fertilization takes place, but he is said (Willcox, 1905: 333) to have admitted later to Willcox that his report was based upon Fischer's comments and not upon his own findings. Further, Dall's statement is said (Willcox, 1905: 332) to have been the authority for that made by Tryon in his *Manual.* Thorson (1935) does provide definite evidence that Fischer's ideas were entirely correct, at least as far as the species *rubella* goes. Thus, for one species, concrete evidence has been presented to indicate that internal fertilization must occur.

Because the evidence is about equally divided on this important issue, it is only possible to say that if internal fertilization, or even fertilization only of eggs from females near by (close fertilization), occurs among the species of *Acmaea* in which speciation is presumed to have occurred following ecologic segregation, then speciation here may have progressed by the usually recognized method of gradual selection of adaptive characters. If, however, fertilization should be shown to take place in the water, at any distance from the parents, between eggs and sperm washed about in the currents, then apparently the only possible explanation for the origin of many of the species discussed in this paper would be one something like that suggested by Goldschmidt (1933: 543). A single mutation which would produce changes sufficiently extensive to prevent interbreeding with the parental form would be necessary. If such a mutation occurred in both a male and a female (assuming cross fertilization) in the same locality at the same time (not impossible in the case of animals with such enormous numbers of progeny and such limited dispersal), or took place in the sex chromosome, a new species could thereby be established, with additional changes accumulating in time.

Only in the event of internal or close fertilization would there be any need for ecologic isolation to permit establishment of the new species, but the influence of such isolation would affect the trend of evolution in either case. In the subsequent discussion, arguments in favor of isolation creating the requisite conditions for speciation are understood to apply only if fertilization is internal or close. Since no special conditions would be necessary where speciation has been by the method suggested for distant fertilization, if it ever occurs, no argument is advanced in the individual cases.

Consideration of the manner in which ecologic segregation and selection proceed indicates that this type of speciation may only occur where the ancestral species possesses much adaptability and a wide range of variation, that is, in those species which are eurytopic in nature. Even more obviously, it will usually result in the formation of species of greatly reduced variability. Thus, the tendency in genera in which the type of speciation produced by ecologic isolation has been active must, in general, be from the variable and eurytopic to the nonvariable and stenotopic, whereas in speciation based on geographic isolation there need be no great reduction in either variability or ecologic tolerance, although sometimes there is. There may even be an accumulated increase in variability in races produced as a result of geographic isolation.

ILLUSTRATIONS OF THE SPECIATION PROCESS IN *Acmaea*

As already stated, speciation caused by ecologic and geographic isolation is well illustrated in the genus *Acmaea.* Several examples have been selected and are presented. Speciation based on geographic isolation is best exemplified by polytypic species in which the process of evolution may be going on at the present time. There are at least two polytypic species of *Acmaea* in North America today. In one of them, the geographic races have, in the past, been considered to be valid species, namely *testudinalis* (Müller) and *scutum* Eschscholtz. Actually, these forms can be shown to be two geographic races of the species *testudinalis* (Müller). The race which has been known as the species *testudinalis* occurs along the North Atlantic coasts of Europe, North America, intervening islands, and coasts of the Arctic circle. The race which has been called the species *scutum* Eschscholtz occurs along the Pacific shores of North America from San Pedro, California, to Alaska. North of the Alaska Peninsula, in the Bering Sea, are individuals intergrading in every possible character, individuals which could as well be placed in one as in the other of these two so-called species. Furthermore, examination of the radular ribbon of these two species reveals slight variation. The general pattern is the same, with such differences in proportions and shape as would suggest that differentiation is progressing along different lines in the two groups, but as yet there has been no break or separation between them. Radulae of specimens from the region of intergradation are intermediate in type between the two extremes, a fact which bears out the evidence derived from the shells.

In view of these facts, there is only one possible interpretation of the relationship between these two forms. Instead of two valid species, there are two geographic races of one species. The very extent of this polytypic species, not with regard to number of races but with regard to geographic range, has served to mask its true nature, although more than once it has been stated that the two so-called species undoubtedly were subdivisions of one species (Dall, 1879: 340; Tryon and Pilsbry, 1891: 11).

Acmaea fenestrata (Reeve) is another polytypic species of the Pacific coast of North America. In the northern part of its range, from Alaska to Cayucos, California, the external color pattern is of plain dark slate gray; the aperture is subcircular in shape; the interior is usually suffused throughout with shades of brown. In the southern part of its range, from Point Concepcion, California, southward, the external color pattern is a regular dotting of cream-color pin-point speckles upon a gray-green background; the aperture is definitely oviform; the interior has a small brown apical spot and a narrow brown border, with a blue intermediate area having but little if any brown suffusion. The difference in appearance between these two geographic races is superficially so striking that one would never suppose them to be races of the same species. However, the radular ribbons reveal that they are of fundamentally the same pattern in both instances, with an exaggeration of some features and certain proportions in one but not the other. These are only such differences as might be expected in two diverging lines. Since intergrades between the two races, found between Point Concepcion and Torro Creek, near Cayucos, complete the polytypic-species arrangement, the southern race should be called *fenestrata fenestrata* (Reeve), and the northern race *fenestrata cribraria* (Gould).

These represent the only two polytypic species of the genus *Acmaea* known at the present time in North American waters, although there are several other species which show evidence of having originated by the method of geographic isolation.

Along the Pacific coast of North America are, among many others, four species of *Acmaea* of which the radular ribbons indicate close relationship. These species, *digitalis* Eschscholtz, *scabra* (Gould), *conus* Test, and *limatula* Carpenter, are distinct, since neither shell characters nor radular ribbons ever intergrade. A careful study of the geographic distribution, microhabitat, and adaptive characters of each of these leads to the conclusion that three of them have descended from a polytypic species originally of two races, one of which later split into two additional races (see below) by the process of geographic segregation. The fourth species, *limatula*, appears to be the result of speciation by a process of ecologic isolation and selection (see below). Before discussing the evidence for speciation by ecologic isolation and selection in this group, I think it best to discuss the evidence in favor of the more familiar speciation of *digitalis, scabra,* and *conus* through geographic segregation.

The range of *digitalis* extends from the western extreme of the Aleutian islands, Alaska, to the southern tip of lower California, a distance of more than four thousand miles. The microhabitat, near high-water line, includes the following factors: (1) microscopic algae for food; (2) cracks, depressions, crevices for shelter; and (3) a minimum of submersion. Throughout a great part of the range (Alaska to Puget Sound), this species meets with no competitors of the same genus, but south of Puget Sound it must compete with *scabra,* its nearest relative, which occupies essentially the same microhabitat. *A. scabra* occurs from Puget Sound in the north to the southern tip of Lower California. The numerical occurrence of *digitalis* and *scabra* along their mutual range throws some light upon the situation. *A. digitalis* is very abundant as far south as Point Arguello, California, but becomes progressively less abundant at localities farther south. *A. scabra* is scarce at most localities along the coast north of San Francisco Bay. Equal numbers are present at localities southward from San Francisco as far as Point Concepcion, in which region *scabra* becomes the more abundant species, remaining so as far south as the region of La Jolla. In addition, a third species, *conus* is present at Point Concepcion, California. This species also occupies essentially the same microhabitat as the foregoing two, and competes with them from this point southward. It appears in progressively increasing numbers at San Pedro and Laguna Beach, although it is relatively scarce north of La Jolla. At La Jolla, San Diego, and more southern localities, it is the most abundant species in this microhabitat. Thus, the three species must have arisen by geographic segregation, since they occupy essentially the same microhabitat in three successive areas, but domination in each area is by a different species. In spite of the present extensive overlap of their ranges, the species concerned have different population and range midpoints (Schenk and Keen, 1936: 924–26), and hence probably had at one time three distinct ranges. Perhaps *digitalis* once ranged from Alaska to San Francisco, *scabra* from Monterey to Point Arguello, and *conus* from San Diego southward. Separation could easily have been effected by the existence of such barriers as long stretches of sandy beach, especially if combined with strong outgoing currents, such as undoubtedly existed at the Santa Cruz-Monterey submergence, and probably at the Santa Clara submergence. Either one of these factors alone might have been sufficient to effect local isolation of the forms on either side of the affected area. Under such conditions, geographic races already in existence could have completed their differentiation into species. If the supposed one-time isolation was later eliminated, the subsequent dispersal of the recently differentiated species would account for the present overlapping of their ranges. This is especially probable inasmuch as no one of the species appears to have gained any particular adaptive advantage over the others, except possibly that of greater tolerance to cold temperature (*digitalis*) or warm temperature (*conus*). The present distribution of these species is, undoubtedly, attributable to the fact that *digitalis* is more eurythermal than is either *conus* or *scabra.* This is indicated by a comparison of the distribution of *digitalis,* which is continuous from the Aleutian Islands, Alaska, to the southern tip of lower California, with that of *scabra,* which extends only from Puget Sound to the tip of Lower California, and, in addition, is very spotty throughout the northern end of the range, with numerous populations only where the temperature of the water is higher than in the region in general. Temperature tolerance limitations are likewise indicated for *conus* by its distribution, which extends from Point Concepcion to the tip of Lower California, with the species becoming abundant only where the water temperature is both high and relatively uniform, as at San Diego.

The range of *limatula,* the fourth species of this group, extends from Crescent City, California, to the southern tip of Lower California, and around into the Gulf of California, at least as far as La Paz. It does not, however, occupy the same microhabitat within that range as is occupied by the other three species already discussed. Furthermore, it only becomes abundant at Monterey, California (the occurrence north of that locality is spotty, the species being abundant only where water temperature is high), and remains so as far south as its range extends. Thus, that part of its range in which it is very abundant coincides in part with the region in which *digitalis* and *scabra* compete on equal terms, in part with the region in which *conus* dominates both. It is difficult to conceive how *limatula* could ever have been geographically separated from these related species and yet at present occupy a range which is coincident with part or all of that of each of the other three species.

Consideration of the probable taxonomic relationships of these species to one another makes the problem of their speciation even more difficult to solve upon a geographic basis. *A. digitalis,* the presumable ancestor of the group, lacks pigmentation on the sides of the foot, whereas the feet of *scabra, conus,* and *limatula* are pigmented. In spite of this common character, probably nonselective, these three species do not show evidence of either simultaneous or successive origins. The radular ribbon of *scabra* is most like that of *digitalis,* whereas that of *conus* is midway between the ribbons of *scabra* and *limatula;* the latter is least like that of *digitalis.* The shells of *conus* and *limatula* are most like those of *digitalis* in that all possess a lustrous internal finish, probably a nonadaptive character, whereas *scabra* has a unique opalescent finish of the interior surface. Still more complicating in implication, the exterior of the shell of *limatula* resembles that of *scabra* more than it does any other, since both have ribs elaborated by spinulescent ornamentation, whereas both *digitalis* and *conus* have plain, rounded ribs. These facts appear to indicate that the three species, *scabra, conus,* and *limatula,* must have descended from an offshoot race of *digitalis* which had undergone pigmentation of the side of the foot, and, further, that *limatula* must have split off before *scabra* and *conus* had become distinct, since it has some characters in common with each, and, in addition has a geographic distribution indicating temperature tolerance equivalent to the combined tolerance of the other two species. The implications of these facts make speciation of *limatula* based on geographic isolation seem impossible.

Consideration of the microhabitat of *limatula* throws light upon the problem of speciation, however, and suggests a process of ecologic segregation and selection. *A. limatula,* as mentioned above, does not occupy the same microhabitat as do *digitalis, scabra,* and *conus.* This species occupies what may be described as essentially the intermediate intertidal zone, in contrast to the high intertidal zone in which the other three species thrive. The intermediate intertidal zone provides macroscopic algae as food, in addition to the microscopic film of algae of the high zone. It is the same zone, and an equivalent microhabitat within the zone, as that occupied by *testudinalis scutum. Acmaea limatula* must, therefore, compete throughout much of its range with *t. scutum.* Survival in a microhabitat such as the one occupied by *limatula* depends upon entirely different adaptations than in the microhabitat occupied by the related species, *digitalis, scabra,* and *conus.*

Adaptations for resistance to desiccation are essential to survival in a microhabitat near high-water mark. In species of the genus *Acmaea,* the most usual adaptations toward this end are (1) elevation of the shell, which permits reduction in diameter and hence size of the aperture, and (2) development of a strong homing habit or instinct (Wells, 1917; Hewatt, 1940), which permits growth of the shell to fit the irregularities of the rock, resulting in better retention of moisture. Unfortunately, the value of Wells's findings was greatly limited by the utter impossibility of identifying his species.

In addition to resistance to desiccation, and partly because of the nature of the adaptation to that end, shelter is a great necessity to animals living near high-water line. This need is aggravated by the greatly increased activity of water in this region. The homing instinct helps in this respect, increasing likelihood of the return of the wandering individual to effective shelter. The reduced size of the foot and aperture also assist, since they make available much smaller crevices or depressions.

With regard to the cause of the first of the above adaptations, increase of elevation, Orton (1932) has offered some suggestions. He believed that increased elevation is solely due to constant tension of the foot muscles for maintenance of adhesion and hence is merely a secondary result or corollary of exacting conditions of the environment lasting over a period of time.

Briefly, his theory is to the effect that animals in positions where exposure to desiccation is frequent and of long duration must spend much of their time with foot muscles tightly contracted in order to hold the shell close to the substrate; this action contracts the mantle edge, thus causing deposition of the shell in a small circumference. This limits growth in diameter at the same time that it forces growth in a vertical direction. Animals in locations at which factors enforcing continual tension of the foot muscles are not in evidence may spend much of their time with foot muscles relaxed. In this condition the foot would be spread out, and shell deposition by the relaxed mantle edge would occur in an ever-widening circle, with little or no vertical growth. This theory seems to offer a sound explanation for much of the variation in height-to-width proportions within a species, and for all of such variation exhibited by individuals.

Obviously, it is not the only explanation necessary, since it will not account for the consistent difference in elevation between certain species; for the elevation in such a species as *persona,* which is not only considerably elevated, but also has a very large aperture, nor for the rigid restriction to limited intertidal zone areas of species with certain height-to-width proportions (as elevated *digitalis* to high zone, flat *t. scutum* to a low zone).

These differences indicate that there must be a certain amount of hereditary limitation of the elevation attainable by an individual of any given species, as well as a hereditary tendency toward increased elevation of the shell in certain species, decreased elevation in others. It is only such a hereditary tendency which could limit the vertical distribution of a species in relation to shell elevation. Furthermore, the increased shell elevation and reduced diameter of certain low intertidal zone species cannot be explained as a response to increased tension. *Acmaea insessa* and *instabilis* possess these characters to a marked extent, yet both live in microhabitats in which tight adhesion is unnecessary most of the time, due to the great fluidity of the substrate of floating plants and to the almost total lack of exposure to desiccation in such a location.

In addition, I find it difficult to agree with Orton's statement that "the organism depends upon the surroundings for its characters." As far as an indirect dependence (survival of only the suitably adapted individuals) goes, and as far as development within limits controlled by hereditary tendencies goes, I can agree with him, but after a careful study of the large group concerned here, I cannot admit the unreserved application of the statement.

Individuals of *limatula* with adaptations for resistance to desiccation, with the concomitant increase in height, would have little chance of survival in a habitat where water action is severe. Since desiccation is not a factor in this habitat, individuals with an architecture such as that of *limatula* not only have a chance of surviving, but may be the only successful type. The architectural pattern of *limatula* is characterized by a depressed apex and a large aperture, similar to that of *t. scutum,* the species with which it presumably competes through part of its range. Such a shell offers virtually no resistance to water impact, and at the same time permits a large adhesive surface, releasing the animal from the need for special shelter. Even the lack of any homing behavior, characteristic of these species, is probably an advantage, since the animal feeds when the tide is at flow. At any time when the force of water impact increases unduly, the animal needs merely to clamp down wherever it is, thereby reducing resistance to the water to a negligible minimum at the same time that the full adhesive power of the large foot surface is made effective. Such a behavior trait is, of course, of greater value to a species feeding during submersion than a homing trait by which the animal attempts to reach some more or less distant spot.

Other facts concerning *limatula* and related species make the likelihood of speciation by ecologic segregation and selection even more evident. For instance, a few individuals of the species *scabra* may be found at a much lower vertical level than is the bulk of the population. Such individuals are always those which vary in the direction of a depressed shell architecture, enlarged aperture, and reduced sculpture. It is not hard to imagine that some such extreme variants of a high intertidal zone race, not likely to survive within the normal limits of the parental microhabitat, may have taken hold in a microhabitat in the lower vertical zone, where ecologic conditions were prohibitive to all individuals of the parental species except such variants. Owing to the ecologic exclusion of all but similar variants, the effective though small distance providing isolation, the rigid ecologic elimination of all but similar progeny which must take place, and the very limited motility of individuals, a high degree of selection should ensue, which might fairly rapidly (geologically speaking) result in speciation, providing some of the variations were hereditary. No matter how long interbreeding should remain possible between the old stock and the new, the likelihood would be greatly reduced because of the rigid reciprocal exclusion of each stock from the microhabitat of the other and the small but effective distance separating their respective areas. Such a process of speciation, in which the isolation of the new stock depends upon purely ecologic factors, and/or in which the process of selection of genetic characters has been solely one of elimination by ecologic agencies of unsuitable characters through failure of individuals possessing them to survive, is obviously based on ecologic segregation and selection.

Further examples of speciation by ecologic segregation and selection have been chosen from two other groups of species occurring on the west coast of North America, each group providing several examples. One of these groups appears to center about *Acmaea pelta* as the original eurytopic species. It includes the species *pelta, asmi, instabilis, ochracea,* and *triangularis,* the four last-named being stenotopic divergents from the first, of which the range both north and south extends as far as, or farther than, that of any of the four descendant species. In this connection, the unusual adaptability of *pelta* and its resultant highly eurytopic nature are important, since presumably only from such material could four species of very different ecologic adaptations have arisen.

The geographic range of *pelta* extends from Yokohama, Japan, across the Aleutian Islands, and down the west coast of North America as far as the southern end of Lower California. It is significant that this, the most eurytopic of North American species, has also the most extensive geographic range. *A. asmi,* closely related to *pelta,* is rigidly stenotopic and has a somewhat more restricted geographic range. Its northernmost record is Sitka, Alaska, and I have had specimens from as far south as San Quintin Bay, Lower California. That part of the range in which the species is most abundant is the same territory in which *pelta* is likewise most abundant (Sitka, Alaska, to Point Concepcion, California). Here again is a type of speciation difficult to explain satisfactorily upon a basis of geographic isolation, but which appears logical when considered to be the result of ecologic segregation and selection.

A. asmi is practically limited to existence upon the snail *Tegula funebralis* (Adams) by the peculiarities of its structural adaptations. The snail occurs in the high intertidal zone on rocky flats, in the crevices, and in shallow pools. The shell of *A. asmi* is very small with a small aperture, extreme elevation of the apex, and some lateral compression. Individuals with these traits would be subject to easy detachment by water impact in the *Tegula* habitat, if it were not for the fact that they are almost always upon a snail (F. H. Test, 1945; A. R. Test, 1945*c*) which tends to keep in protected spots, and serves as a shock absorber, partly nullifying the effect of water movement. Since it would only be possible for a very small animal with a small aperture, and hence limited adhesive surface, to maintain position upon the rounded surface of this host snail, animals which grew before sexual maturity to anywhere near the usual size of adult *pelta* would be forced to leave the snail and attempt to find suitable substrate elsewhere before maturity. This would result in automatic elimination of such extreme variants, since suitable substrate for large animals of this type is not available within the limits of motility of these animals. Further, and perhaps of more immediate import, only animals so modified in their feeding habits that they could and would subsist upon microscopic algae could attain maturity in this microhabitat. The reproducing population must have been drawn from those extreme variants of the ancestral species which fulfilled these specifications, all others being automatically eliminated by natural selection, as suggested above. Thus, almost immediate isolation of the occupants of the new microhabitat would result, since the habitat described is not adjacent to that of *pelta*.

The nearly total lack of individual variation in *asmi* indicates that the elimination of unsuitable variants by selection must be rigid. Completion of the speciation process from such extreme and segregated variants, as already suggested, could be very rapid (again, geologically speaking). All specimens of *asmi* are black, with sculpturing consisting of fine riblets and grooves. I have never seen a specimen within the ordinary confines of the species habitat with any external color variation, although specimens with white interiors are occasionally encountered. The latter variation could have no selective value, hence it is not eliminated. The apparently rigid elimination of external color variants, which could only be due to predators hunting by sight, has resulted in protective coloration to the extent that limpets of this species appear to be a part of the host's foot. Possible predators upon limpets include various birds (Henderson, 1927: 178; Bent, 1929: 308, 313, 322; Munro, 1936: 234; Vallentin, 1924: 308–9; Cottam, 1939: 36, 60, 77, 94, 129), rodents, raccoons, and perhaps crabs. These facts make it difficult to explain speciation in this instance by any process other than that of ecologic isolation and selection.

Another species related to *pelta* is *instabilis*. It has a much less extensive geographic range, encompassed by that of *pelta*, and extending only from the northern end of Vancouver Island to Monterey. This species is stenotopic, its microhabitat being limited to the fronds and stipe of the alga *Laminaria Andersonii* Farlow. Individuals of the species are large, as plant-dwelling limpets go, with a rocker-like margin resulting from a marked downward inclination of the sides of the shell as a correlative of extreme lateral compression. This rocker-like margin enables the animal, which moves and adheres lengthwise of the stalk, to fit snugly upon the rounded substrate provided by the subcylindrical stipe of the host plant. The shells of this species are always of a peculiar brown color and horny texture, giving them a striking resemblance to the plant upon which they live. The factors involved in the origin of this species appear to have been somewhat different from those involved in the instance previously described. The substrate plant does not seem to offer any topographical peculiarities which are not likewise offered by *Postelsia*, upon which specimens of *A. pelta* are frequently found. Indeed, if casually examined, the specimens of *pelta* upon *Postelsia* usually structurally resemble the architecture of *A. instabilis* closely enough to be confusing. *Laminaria Andersonii*, however, does not appear to be acceptable food to *A. pelta*, or else the microhabitat represented by it, falling below the low-water line, is too low for *pelta*, or both. Only on the rarest of occasions are specimens of *pelta* taken from this species of *Laminaria*. It is readily conceivable, however, that perhaps at some time when desirable foods were at a mininum, some individuals of *A. pelta* which would or could tolerate *Laminaria Andersonii* as food and were able to stand the greater depth and reduced length of exposure invaded the vacant microhabitat upon this particular plant, and then developed ontogenetically and phylogenetically along the lines necessary for existence upon such a substrate. Evolution of the population of *A. pelta* variants upon *Laminaria Andersonii* along stenotopic lines could have proceeded readily, because of prompt elimination of all variants except the extremes best suited to the microhabitat in question and isolation by the sand around the holdfast from the rocks on which *pelta* is found. The apparent unsuitability of the microhabitat for most members of the parental species would serve as a barrier to interbreeding, assuming close fertilization to take place, since only such variants as those providing the nucleus for the nascent species could survive in the microhabitat. Thus, nearly complete isolation of the nascent species is conceivable.

Equivalent processes can be imagined for the other two species of this group, *ochracea* and *triangularis*, each along its own pecular lines. It seems more profitable to consider the process as it has occurred in another group of species in which the ecologic factors determining speciation have been still different.

The group of related species remaining for consideration centers about the *testudinalis* polytypic species, in particular the geographic race or subspecies *testudinalis scutum.* As already mentioned, the present-day races of the *testudinalis* species are an indubitable product of geographic isolation. Closely related to them are species which have also undoubtedly originated by the method of geographic isolation, such as *schrenkii* Lischke in Japan, *pileopsis* (Quoy and Gaimard) in Australia, and *badia* (Oliver) in New Zealand. In addition, there are several species, *persona, fenestrata, insessa,* and *palaecea,* of which the ranges are entirely or partly coincident with that of *testudinalis scutum* and which appear to have separated by ecologic segregation and selection rather than from a process of geographic segregation.

A. testudinalis scutum occupies a microhabitat essentially in the intermediate intertidal zone, but extending part way into the high and beyond the low intertidal zones. In this microhabitat, the algae *Enteromorpha* and *Ulva* serve most importantly as food. Certain factors are notable for their absence. For instance, danger of desiccation is greatly reduced or absent, permitting development of an enlarged aperture which, in turn, permits depressed architectural structure. Since special provisions for shelter are absent in this microhabitat, the depressed architecture has considerable survival value. Inasmuch as the subspecies *scutum* of the *testudinalis* species is eurytopic and possessed of considerable adaptability, individuals which are structurally extreme radiate beyond the normal confines of the microhabitat, providing material for speciation through ecologic isolation.

Another polytypic species, *fenestrata,* seems closely related to *testudinalis scutum.* This second polytypic species has a geographic range entirely coincident with that of *testudinalis scutum,* extending from Unga Island, Alaska, to San Pedro, California. *A. fenestrata* and *testudinalis scutum,* however, do not occupy the same microhabitat. Both geographic races of *fenestrata* occupy a microhabitat in the high intertidal zone (never extending lower) comprising only microscopic algae as food, and having as active factors frequent danger of desiccation and subjection to severe abrasion because of the large amounts of sand in the water. Such a set of factors requires peculiar adaptations, both of structure and behavior.

Some adaptation to reduce the danger of desiccation becomes essential. This is accomplished in the races of *fenestrata* by a partly reduced aperture and an associated increase in elevation, together with a behavior trait: as the tide recedes, the individuals proceed down the side of the rock until covered by the sand at its base. At night the animals do not move down. Also, occasionally, when the sun is in such a position that the light is evenly distributed on all sides with reference to the animal's location, the limpet fails to move; hence, this must be a weak negative phototropic response. Apparently, the limpet, as the water recedes and the light becomes brighter, moves down the side of the rock, keeping within the area of subdued light. This trait serves, incidentally, to obviate two other dangers. The bareness of the rocks inhabited by this species would make the animals, if exposed by the tide, fairly obvious prey to any predator hunting by sight. Also, maintenance of adhesion during the ebb and flow of the tide, with the accompanying increase in water impact, might be endangered if the animal should remain in an unprotected location on the bare rock. The increased thickness of the shell is probably the most important adaptation for withstanding the abrasive action of the loose sand in the water, aided by the conical shape, and the burying trait at periods when the sand action is most severe.

The species *fenestrata,* then, although it shows no evidence of ever having had a geographic distribution distinct from that of *testudinalis scutum,* seems to have originated within the latter's range. It also exhibits striking ecologic adaptions which may have had their origin in extreme variants of the ancestral race better able to survive in the particular microhabitat occupied by the *fenestrata* group. This microhabitat, untenable to normal individuals of the ancestral race, would provide the requisite isolation for speciation, especially since the increased elevation of the variants would prevent their dispersal back into the ancestral microhabitat. The isolation thus provided should offer the necessary condition for speciation to proceed, and hence here again species formation would be due to ecologic isolation and selection.

Another species, *persona,* which is also related to the race *testudinalis scutum,* offers just as good evidence of speciation by a process based on ecologic isolation. The range of *persona* extends from the Shumagin Islands, Alaska, to Monterey, California, not as far north nor as far south as the more eurytopic *testudinalis scutum.* A study of the ecologic adaptations of the stenotopic descendant, *persona,* again suggests ecologic segregation and selection. The microhabitat of *persona* is very limited in contrast to that of the eurytopic ancestor. The microhabitat, besides being more limited, is very different from that of the ancestral species, occurring in a different intertidal zone. It is limited to the high intertidal zone, comprises microscopic algae as food, and is confined to situations where the light is reduced, such as the undersurfaces of rocky ledges, roofs of caves, and deep crevices.

In locations of this type, certain factors differ decidedly from those affecting the ancestral *testudinalis scutum.* Danger of desiccation is increased because of increased frequency and length of exposure, but the very nature of the locations utilized (see above) limits the extent of this danger. Force of water impact is considerably increased. Danger from predators is greatly reduced by the low visibility. Hence, it is possible for occupants to meet the exigencies of the microhabitat by adaptations other than those encountered thus far, since the differing combinations of ecologic factors change the problems involved in selective elimination. As a result of lack of danger from predators large size is less a liability than in the species previously discussed. Because of some danger of desiccation, increased elevation is desirable. The combination of increased size and increased elevation permits an enlarged aperture, which is not too great a liability in the situation concerned because of protection from sun and wind. Increased elevation, usually an eliminating factor where water impact is great and no special shelter from it is available, is compensated for by other features, namely, large increase in adhesive power due to the large foot surface correlated with the large aperture, and a streamlined architecture. The shells of this species have an outstanding feature, a long, arched, posterior surface which is always oriented to receive the impact of the water. The long arch is structurally sound for the reception of severe stress, and at the same time serves actually to break the force of the impact by its streamline.

In addition, certain behavior traits are essential to the success of the species in this microhabitat. The animals feed only at low tide, and when light at the feeding grounds is very dim. This is feasible since, in this microhabitat, such a set of conditions occurs frequently. With the first persistent splashes of returning tide, or suggestion of increasing light, the animals return to their roosting sites, where they clamp down tightly and remain until conditions are again right for feeding. Since their food (microscopic algae) is abundant and competitors are very few, there is little or no difficulty with regard to obtaining sufficient food in the time available.

Evolution of the architectural structure through ecologic segregation and selection is relatively easy to postulate in this species. The type of sculpture has not deviated far from that of the ancestral race. The general architecture has diverged considerably, but along lines forecast by variants within the ancestral species. The apex is considerably more elevated and somewhat more posterior than that of the ancestral species. The elongated posterior surface is markedly arched, a feature recognizable as an extensive exaggeration of the slight convexity of the posterior face of the ancestral species. The color pattern is more stereotyped both internally and externally. The size is generally larger, and the shells are thicker and heavier. Presumably, any individuals developing along different lines would very quickly be eliminated from this microhabitat. For instance, the flatter individuals characteristic of the ancestral race would die by desiccation during the frequently repeated and relatively long exposures; those with elevation, but no long gently arched surface to ease the water impact would quickly be forced from the rock, or smashed. Individuals with the architectural pattern of *persona* are most unlikely to survive or succeed in other microhabitats. Hence, it is obvious that variants of the ancestral race which were extreme enough to invade such a microhabitat would be truly isolated from the parental species by a large part of the intertidal zone. Speciation could take place by the active selection of the most suitable architectural type. Selection must proceed continually in such a habitat.

DISCUSSION

From these examples, and others not discussed here, it has become apparent that in the genus *Acmaea,* in addition to the process of speciation based on geographic isolation, there has been, and perhaps even more frequently, speciation from eurytopic ancestors by the process of ecologic isolation and selection.

Speciation by ecologic segregation and selection can in this group probably only occur from a eurytopic form, and may presumably take place rapidly as such things go. The materials for it are variants of a given eurytopic species, variants so extreme in their deviation from the normal as to make survival in the usual microhabitat of the parental species difficult or impossible. Such variants may actually thrive, however, if they settle in a suitable microhabitat in which, in their turn, normal individuals of the parental species could not survive. Such a situation may result in the virtual isolation of the variant individuals from normal individuals of the parental species, if there is an untraversable barrier between the two microhabitats, and with consequent inbreeding of the variants if internal or close fertilization occurs. Further, all variants in the progeny which revert toward the ancestral form are bound to be eliminated from the microhabitat by the highly selective action of the ecologic factors involved. The result could be the formation of a new stenotopic species having a tendency, because of ecologic segregation and rigid selection, to diverge from the pattern of the ancestral species by accumulation of the variations successful in the new environment. All those ecologic factors which exercise a selective action upon the individuals living in the microhabitat may contribute to the production of the new species. In the event that external fertilization takes place, and the actual differentiation of a species is due to one mutation without necessarily involving isolation, subsequent ecologic isolation together with selection of the more suitable variants would still play an important part in molding the evolutionary trend of the species.

SUMMARY

It has become apparent that in the genus *Acmaea,* in addition to the process of speciation based on geographic isolation, there has been, perhaps even more frequently, speciation from eurytopic ancestors by the process of ecologic isolation and selection.

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